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PRELIMINARY REPORT OF CROSSING TWO HEMIPTEROUS SPECIES, WITH REFERENCE TO THE INHERITANCE OF A SECOND EXCLUSIVELY MALE CHARACTER.

KATHARINE FOOT AND E. C. STROBELL.

OXFORD.

Attention of cytologists has been centered during the past few years on the chromosome theory that claims to offer an explanation of sex-determination—a theory due to the discovery of certain morphological differences in the chromosomes of the males and females of many species. This discovery is responsible for the chromosome hypothesis of sex-determination—an hypothesis that awaits the test of experiment.

Recently (Foot and Strobell, '13) we published the results of some cross-breeding experiments undertaken with the aim of testing the above mentioned hypothesis that the factors determining sex are carried and distributed by definite chromosomes. The character selected to test this hypothesis was an exclusively male character in *Euschistus variolarius*—a distinct dark spot which is present on the genital segment of the male only, and we claimed that the method of the transmission of this spot should be an index of the method of transmission of the entire male genital segment. This exclusively male character—the genital spot—is a distinguishing feature of *Euschistus variolarius*, but is absent in *E. servus*. We therefore selected these two species as well adapted to test the function of the so-called sex-chromosomes in the transmission of this exclusively male character. Our claim that the method of transmission of the genital spot may be interpreted as an index of the transmission of the male reproductive organs themselves has not been accepted by two critics (Morgan and Doncaster) who have recently referred to our results. In reply to the criticism of these two advocates of the chromosome theory of sex-determination, we quote the following from a paper now in press (Foot and Strobell, '14b).

"After this paper was sent to press a notice of our results appeared in the following publications: 'Heredity and Sex,' Morgan ('13), and 'Chromosomes, Heredity and Sex,' Doncaster, *Q. J. M. Sci.*, Vol. LIX. ('14).

The latter disposes of our results in a footnote, as data irrelevant to a paper entitled "Chromosomes, Heredity and Sex—A Review of the Present State of the Evidence with Regard to the Material Basis of Heredity, Transmission and Sex-Determination."

From his report of the evidence he draws the following conclusion:

"The facts of sex-limited<sup>1</sup> transmission thus support the hypothesis that both ordinary Mendelian factors and the sex-determining factor or factors are borne by chromosomes," p. 511, and in the above-mentioned footnote he adds: "The recently published work of Foot and Strobell cannot be used as an argument against this proposition. They have shown (as was previously known in birds and moths) that a secondary sexual character in Hemiptera can be transmitted through the sex that does not show it; but the character was not sex-limited<sup>1</sup> in transmission; their results, therefore, have no bearing in the present discussion." As opposed to this decision we claim that the very fact that the genital spot is not linked with one of the so-called sex chromosomes is a point that calls for a satisfactory explanation by those who believe in sex-determining chromosomes, and our results cannot be cancelled by a dogmatic assertion that they have no bearing on the subject.

Morgan treats the facts with more consideration and attempts to give an explanation of them, though his explanation appears to us more as an attempt to excuse the facts than to explain them. Part of his explanation is merely a restatement of our conclusions, and the remainder is not in harmony with the facts.

We concluded that our results demonstrate that the spot can be transmitted without the X- or the Y-chromosome and Morgan accepts this as follows, "these results may be explained on the assumption *that the factors lie in other chromosomes than the sex-chromosomes.*"<sup>2</sup>

<sup>1</sup> Sex-limited is used by Doncaster in the sense that sex-linked is used by Morgan.

<sup>2</sup> The italics are ours.

We concluded that if one assumes (for the sake of the argument) that the spot factors are in a diploid pair of chromosomes, it becomes necessary to assume other factors outside the chromosomes. We called such hypothetical factors "inhibiting factors" and we said of them: "We are forced to admit that inhibiting factors—whatever they are—must be located outside the chromosomes, in the region of pure hypothesis."

Morgan appears to accept this, calling such hypothetical factors "*things in the cell*," and symbolizing them as A. B. C. He says "the result (or character) that a factor produces depends on its relation to *other things in the cell* (here A. B. C.)," and he adds, "We are dealing, then, not with the relation of X to S *alone*, but this relation in turn depends on the proportion of both X and S to A. B. C."

In the above-quoted paragraph he includes in his explanation the assumption of a relation between the spot factors and the X-chromosome, and this we believe is a part of his explanation which is not sustained by the facts. The spot can be transmitted directly from the male to his male offspring—and therefore this must be by the male-producing spermatozoön—if there is such a thing and the so-called male-producing spermatozoön has no X-chromosome. It is impossible to believe that in such cases the inheritance of the spot is dependent upon the relation of the spot factors of the sperm to the X-chromosome in the egg, especially if the cross is made with a pure *servus* egg. Morgan evidently thinks this is possible, however, for in his explanatory diagram he illustrates a cross between *E. servus* ♀ × *E. variolarius* ♂, a cross which we explained we were unable to attempt on account of scarcity of material.

His diagram, if assumed to be an explanation based on the facts of our experiments, is further in error in its illustration of the F<sub>1</sub> hybrids. In his simple Mendelian scheme all the F<sub>1</sub> hybrids are illustrated as typical heterozygotes and the fact is ignored that two out of the eleven of our F<sub>1</sub> hybrids are like *servus* in having no spot. If such a modification of the spot can be caused by "*other things in the cell*," it would seem that merely calling these "A. B. C." is no explanation of the results.

Morgan excuses his attempted explanation on the ground

that we have failed to explain our results. We make no apology for this. We believe the duty of the scientist is to curb the natural temptation to force an explanation of individual results, for science to-day is overburdened by premature and undigested generalizations. We would aim rather to follow the example of those scientists who are willing patiently and conscientiously to collect data sustained by the hope that some day the facts may be of value.

Both Morgan and Doncaster class the genital spot of *variolarius* with the secondary sexual characters of authors and they therefore interpret our results as not having the bearing on the theories of sex-determination which we claim for them. Now our claim has been that the genital spot of *variolarius* is an integral part of the male genital segment—the structure of the female genital segment being such that the spot could not be present in this segment without changing the form of the segment itself—and we have claimed that therefore a study of the transmission of the genital spot should give a trustworthy indication of the method of transmission of the entire genital segment.

This claim that the method of transmission of the genital spot should be an index of the method of transmission of the genital organs of the male, has been completely justified by further work on these hybrids.

In the present paper we shall report the results from the study of the transmission of a second exclusively male character, and it seems to us that these results cannot be set aside as having no bearing on "Sex and Heredity," for this second exclusively male character is the male genital organ itself—the intromittent organ. The genetic results from our study of the genital spot of *variolarius* may be open to the criticism that as the spot is "not directly connected with the act of reproduction" it should be classed with the secondary sexual characters; but the intromittent organ is certainly free from such criticism and can be justly classed as a primary sexual character: In view of the fact that our results from the study of the transmission of the *variolarius* spot have been set aside on the ground that the spot is a secondary sexual character and therefore has no bearing on the problem of the determination of sex, it is necessary first

to establish the claim that the intromittent organ can be classed with the primary and not the secondary sexual characters. This apparently ought not to be difficult, but a difficulty does arise owing to the fact that recent authors who have discussed secondary sexual characters have avoided defining them and have neglected to state wherein they are to be distinguished from the primary sexual characters.

According to Darwin '59 Hunter defines secondary sexual characters as follows:

"The term, secondary sexual characters, used by Hunter, applies to characters which are attached to one sex; but are not directly connected with the act of reproduction."

Darwin '86 adopts Hunter's classification of primary and secondary sexual characters; but shows that even such an apparently clear cut definition encounters difficulties. He says:<sup>1</sup>

"With animals which have their sexes separated, the males necessarily differ from the females in their organs of reproduction; and these afford the primary sexual characters. But the sexes often differ in what Hunter has called secondary sexual characters, which are not directly connected with the act of reproduction; for instance, in the male possessing certain organs of sense or locomotion, of which the female is quite destitute, or in having them more highly-developed, in order that he may readily find or reach her; or again, in the male having special organs of prehension so as to hold her securely. These latter organs of infinitely diversified kinds graduate into, and in some cases can hardly be distinguished from, those which are commonly ranked as primary, such as the complex appendages at the apex of the abdomen in male insects. Unless indeed we confine the term 'primary' to the reproductive glands, it is scarcely possible to decide, as far as the organs of prehension are concerned, which ought to be called primary and which secondary" (p. 253).

Morgan '13 also appears to accept Hunter's classification, for in his rather full list of secondary sexual characters he includes none that are "directly connected with the act of reproduction." He opens his discussion of secondary sexual characters as follows:

<sup>1</sup> The italics are ours.

### "THE SECONDARY SEXUAL CHARACTERS."

"In the most highly evolved stages in the evolution of sex a new kind of character makes its appearance. This is the *secondary sexual character*. In most cases such characters are more elaborate in the male, but occasionally in the female. They are the most astonishing thing that nature has done: brilliant colors, plumes, combs, wattles, and spurs, scent glands (pleasant and unpleasant); red spots, yellow spots, green spots, topknots and tails, horns, lanterns for the dark, songs, howlings, dances and tourneys—a medley of odds and ends" (p. 26).

If we are to discard Hunter's classification, because it is found difficult to determine into which class some of the characters rightly belong, we should have to be dissatisfied with many classifications that are thoroughly well established.

If we limit the term "primary sexual characters" to the reproductive glands, it offers an escape from the difficulties in classifying the prehension organs, as Darwin has pointed out; but it would seem that greater difficulties are met by refusing to place the intromittent organ in the same group with the reproductive glands; and placing it in the group with characters so far removed from "direct connection with the act of reproduction" as, for example, Morgan's list of secondary sexual characters, "brilliant colors, plumes, combs, wattles, and spurs, scent glands (pleasant and unpleasant); red spots, yellow spots, green spots, topknots and tails, horns, lanterns for the dark, songs, howlings, dances and tourneys—a medley of odds and ends." The intromittent organ is not only "directly connected with the act of reproduction"; but it is as much a part of the sex of the individual as the reproductive glands themselves. Any one of the characters in Morgan's entire list of male secondary sexual characters could appear in the female without changing her sex; but the intromittent organ is as clearly indicative of the sex as are the reproductive glands themselves.

If a definite chromosome carries the factors for determining sex and it therefore carries the factors for the reproductive glands, it would seem logical to suppose that the chromosome carrying the factors necessary for the development of the male reproductive glands would also carry the factors necessary for the

development of the intromittent organ which, when present, is functionally a necessary adjunct of the glands, and as indicative of the sex as the reproductive glands themselves. If we cannot accept the mode of transmission of the intromittent organ as an index of the mode of transmission of the reproductive glands, it would seem necessary to discard all structural features or other characters, which are distinctive of the gonads of a given species, such as their distinctions in size, form, color, etc., and assume that these characters, associated with the gland, have a different mode of transmission from the gland itself.

This would prevent any experimental test being applied to the chromosome theories of sex-determination and leave free scope for the wildest cytological speculations. If we should place the intromittent organ in the group of secondary sexual characters, because it has certain features in common with these characters we ought logically to place the reproductive glands themselves in the same group. For example, both these organs, in common with most of the secondary sexual characters, can be transmitted to the opposite sex—hermaphrodites appearing in forms that are normally sexually distinct. A case in point is Goodrich's '12 interesting and important discovery of a male amphioxus in which 49 of the gonads were testes containing ripe spermatozoa and one was an ovary containing ripe ova. It may be urged that the intromittent organ is a secondary sexual character on the evidence that in the development of the embryo it appears much later than do the gonads—this indicating that the gonads are more fundamental and stable morphological entities. But there are facts opposed to this interpretation—Smith '10 found that when the spider crab is infected by the parasite *sacculina*, the testes can become so greatly metamorphosed that some of the cells may develop into ova and *the same testis* contain *both* ripe ova and spermatozoa.

It would seem that the division between primary and secondary sexual characters in common with almost all attempts at classification, has the objection that the line of demarcation is not, at all points, perfectly clear; but we believe, in spite of this, that we are justified in classing the intromittent organ as a primary sexual character and that the results from the study of the trans-

mission of this organ may justly be claimed as an index of the method of transmission of the reproductive glands themselves.

Before giving these results we would express our great indebtedness to Professor Poulton and to Dr. Eltringham, of Oxford. We are indebted to Professor Poulton for his kind response to our wish to find an experienced entomologist in England who would be willing to study *E. variolarius* and *E. servus* with the aim of finding other characters than the genital spot that could be studied in the hybrids. He kindly suggested Dr. Eltringham, of Oxford, to whom we are indebted for the discovery that there is a marked specific difference in the intromittent organ of *E. variolarius* and *E. servus*. This discovery has made it possible for us to secure the results which are recorded in this paper.

#### RESULTS AND DISCUSSION.

The intromittent organs of *E. variolarius* and *E. servus* differ markedly in their length. We have dissected these organs from the genital segment of many of the parent species, and from all the hybrids, both of the  $F_1$  and  $F_2$  generations. These have been mounted and photographed at a magnification of 20 diameters, and all have been carefully measured at this magnification. The intromittent organ of *E. variolarius* varies in length between 85·5 and 106 mm., while that of *E. servus* varies between 146 and 182 mm. These measurements were made from 62 pure *variolarius* specimens, and from 62 pure *servus* specimens, the mean length of the intromittent organ of *variolarius* being 96·5 mm., and of *servus* 166·41 mm.<sup>1</sup>

Photos 1 to 4 show four typical intromittent organs of *E. variolarius*, these four varying in length between 94 mm. and 98·5 mm. Photos 5 to 8 show four typical intromittent organs from *E. servus*, these four varying in length between 158 mm. and 182 mm. Photos 9 to 12 show four typical intromittent organs of the  $F_1$  generation derived from *E. variolarius* ♀  $\times$  *E. servus* ♂. These four vary in length from 122 to 132 mm. We have ten intromittent organs of this  $F_1$  generation, nine of these being variable intermediates, and one like pure *variolarius*.

<sup>1</sup>A discussion of the mean lengths of the hybrids and of the back-cross, and their bearing on the Mendelian type of inheritance, will be given in a later and more detailed report of these results.

Thus the type of intromittent organ characteristic of the species is transmitted through the female to her male offspring, and also directly by the male, and we may add that this is further proved by the back cross ( $F_1 \text{ ♀} \times \text{pure } variolarius \text{ ♂}$ ). Thus the mode of transmission of this second exclusively male character is like that of the genital spot—*both* of these exclusively male characters being transmitted through the female as well as directly from the male—neither of these characters therefore being sex-linked.

Photos 13 to 20 show eight typical intromittent organs from the  $F_2$  generation, these eight varying in length between 85·5 mm. and 140 mm. A few of these specimens (photos 13–15) show that the factors which determine the genital spot and those which determine the intromittent organ are not linked in inheritance (see below).

In our study of the transmission of the genital spot of *variolarius* (Foot and Stobell, '14a) we divided the hybrids into three groups—those having a genital spot like that of pure *variolarius*, those without a spot like *servus*, and those with a spot intermediate between these two extremes. In order to compare the results from the study of the two exclusively male characters—the genital spot and the intromittent organ—we have again grouped the hybrids into three classes, those having a length of intromittent organ like that of *variolarius*, those with a length of organ like that of *servus*, and those with a length intermediate between these two extremes.

By this grouping it is possible to compare the genital spot of each individual hybrid with the type of intromittent organ of the same hybrid, in order to determine whether these two exclusively male characters are linked in inheritance—to determine to what extent the two are associated in their transmission. Before discussing this point we shall summarize the points of agreement in the inheritance of the two characters.

The intromittent organ—like the genital spot—is not sex-linked, this being shown by the facts that it is transmitted through the female, and also directly from the male to his male offspring. The intromittent organ—like the genital spot—is transmitted without the aid of either of the so-called “sex-chromosomes.” It is transmitted without the aid of the Y-

chromosome because it is inherited through the female, and it is transmitted without the aid of the X-chromosome because it is transmitted *directly* from the male to his male offspring. Like the genital spot, the intromittent organ fails to show dominance in the F<sub>1</sub> generation, and fails to show a simple Mendelian ratio in the F<sub>2</sub> generation; but the details demonstrating these facts must be reserved for our full report of this work, in which it will be possible to compare the inheritance of these two exclusively male characters in every individual of the F<sub>1</sub> and F<sub>2</sub> generations.

As in the case of the genital spot, we are forced to conclude that if the factors determining the inheritance of the intromittent organ are carried by definite chromosomes, they must be in *at least* a pair of diploid chromosomes, and as in the case of the genital spot, we are further forced to conclude that there are factors in the cell, outside the chromosomes, which determine just how many of the factors determining the character of intromittent organ shall find expression in the first and second generations of hybrids. The facts show, as in the case of the genital spot, that this cannot be accomplished by the assumed mechanism of division of the chromosomes, but is dependent upon hypothetical factors outside the chromosomes, and thus the distribution of unit factors through the mechanism of chromosome division seems to be an unnecessary assumption. If the factors essential to produce these two exclusively male characters are confined to one chromosome they can be in the Y-chromosome *alone*, for according to the mechanism of the two maturation divisions this is the *only* chromosome that can be in *all* the so-called male-producing spermatozoa. The facts, however, demonstrate that not only the genital spot, but the intromittent organ, can be transmitted without the aid of the Y-chromosome. If, as the facts demand, the factors for these two exclusively male characters cannot be in less than a pair of chromosomes, there seems no adequate reason for confining them to a single pair, or even to the chromosomes at all, for if factors outside the chromosomes and outside the mechanism of the division of the chromosomes, are responsible for the exact expression or total suppression of these characters, this deprives the chromosomes of a most important function which has been attributed to them, based on the mechanism of their division.

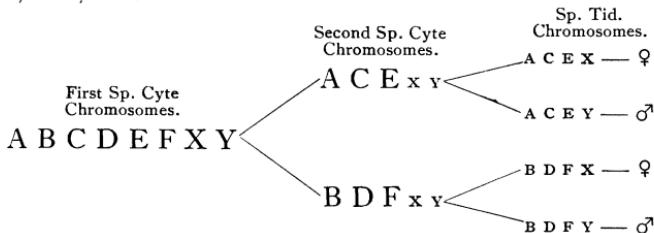
The results from the back cross demonstrate that the type of intromittent organ distinctive of the species can (like the presence or absence of the genital spot) be transmitted by *both* the so-called male-producing and female-producing spermatozoa. The back cross demonstrates not only that the male can directly transmit the intromittent organ distinctive of *variolarius*; but that the type of intromittent organ distinctive of *servus* is transmitted by the  $F_1$  female, and therefore was transmitted by the female-producing spermatozoon of the first cross. If such a primary sexual character of the male can be carried by the female-producing spermatozoon, it is only logical to believe that female primary sexual characters also can be transmitted by both types of spermatozoa (male-producing as well as female-producing)—for it is difficult to believe that male and female primary sexual characters differ fundamentally in their method of transmission. The facts appear to deprive the male-producing spermatozoon of its distinctive function, and challenge the logic of endowing slight morphological differences in structures of the cell with causal attributes of fundamental importance.

*Linkage in Inheritance.*—If factors which stand for a given character are carried by a definite chromosome or pair of chromosomes, and the inheritance of the character is due to a special distribution of the factors at mitosis, it would seem logical to expect that the factors of two characters showing a very special mode of distribution (*i. e.*, exclusively male characters) would be contained in the same chromosome, and that this would be indicated by their being linked in the hybrids. We would expect the absence or presence of the genital spot, distinctive of one species, to be associated in inheritance with the type of intromittent organ characteristic of the same species. Even if the extent to which a character appears is dependent upon hypothetical factors outside the chromosomes, we would expect these hypothetical factors to act equally on two characters which are so closely associated as to be contained in the same chromosome. We should expect the two characters never to be so entirely dissociated that we find, in the same individual, the absence of spot characteristic of one species, associated with the type of intromittent organ distinctive of the other species. Instances of

such complete dissociation do however occur and are shown, for example, in photos 13 and 14, which have the length of intromittent organ characteristic of *E. variolarius* (85·5 mm. and 99 mm.) while the specimens from which these organs were dissected have the *E. servus* absence of spot. Photo 15 has a length of intromittent organ almost equal to *E. servus* (140 mm.), while the specimen from which this was dissected has the genital spot distinctive of *E. variolarius*. There are, however, instances of association in the inheritance of the two characters, the intromittent organ and genital spot typical of one of the species occurring in the same  $F_2$  individual; but exact classification of the full results shows that the two characters are transmitted quite independently of each other. The intermediates, having a large range of variation, make it possible for many of them to appear to show the two characters in the association that would be in harmony with the chromosome hypothesis, but an exact comparison shows that two plus and two minus intermediates are quite as frequently associated as are a plus and a minus intermediate. If we find such independence in the transmission of the two characters, there seems no logical reason for assuming that their factors are carried by the same chromosome. If their frequent independence in transmission forces us to locate them in at least two of the seven chromosomes contributed by each parent, there seems no adequate reason for confining them to the chromosomes at all, especially as their final mode of expression is not dependent upon the distribution at mitosis of unit factors carried by the chromosomes, but upon hypothetical factors outside the chromosomes.

As the advocates of the sex-determination theory may dismiss these results—as in the case of the genital spot—on the ground that the intromittent organ is not sex-linked, and is merely a secondary sexual character, it may be profitable to attempt to follow theoretically the transmission of what must be admitted are *primary sexual* organs, (the ovaries and the testes), while assuming that they are “sex-linked.” This has its difficulties in the case of the testes, for the factors determining the sex-linked characters of authors are assumed to be in the chromosome which is homozygous in one sex and heterozygous in the other

sex. This would place sex-linked factors for the testes in the X-chromosome of these insects; and locating these factors in this chromosome would involve their being in the female-producing spermatozoa only, and this type of spermatozoa therefore would carry the determining factors for *both* the ovaries and the testes, while the male-producing spermatozoa would carry neither the one nor the other. We shall try to show by an analysis of the chromosomes that it is as impossible to associate the testes with the sex-chromosomes as we have shown by experiment is true for the two other exclusively male characters—the genital spot and the intromittent organ. In order to simplify the discussion, we reproduce the following diagram used in an earlier paper to show the method of division of the 14 somatic chromosomes which are distinctive of both *E. variolarius* and *E. servus*. In the diagram we have used the method of designating univalents by the letters of the alphabet, bivalents being represented by AB, CD, EF.



Scheme of the two maturation divisions of *Euschistus variolarius* and *Euschistus servus* based on the assumption that the first maturation division separates autosomes of maternal and paternal origin and the second division halves them. The XY-chromosomes on the contrary being halved in the first division and separated in the second division. The relative positions of the autosomes may be changed unless definite chromosomes are always destined to the same pole, but reversing their position in this regard does not alter the end result—that the only chromosome common to both so-called male-producing spermatids is the Y-chromosome.<sup>1</sup>

The above diagram demonstrates the two types of spermatozoa, those having the X-chromosome—so-called female-producing; and those having the Y-chromosome—so-called male-producing. If we accept Morgan's conclusion that factors determining all sex-linked characters are located in the X-chromosomes and we assume that the primary sexual characters are sex-linked, this involves placing the factors determining both the ovaries and the

<sup>1</sup> Only six of the twelve autosomes are designated.

testes in the X-chromosomes and, as stated above, this would effectually deprive the so-called male-producing spermatozoa of an essential male-producing function. This is so evidently out of harmony with the chromosome sex-determination theory, that it needs no further comment.

If we attempt to place the factors determining the testes in the other sex-chromosome (the Y-chromosome) we meet difficulties that are equally obvious, for there are many forms that have no Y-chromosome at all. If we could ignore this important fact, we would have, in these insects, quite a diagrammatic demonstration of the chromosome sex-determination theory, for the Y-chromosome is the *only* chromosome that is in *all* the male-producing spermatozoa, just as the X-chromosome is the *only* chromosome that is in *all* the female-producing spermatozoa. Each is the *only* chromosome which is distinctive of the type of spermatozoa which it identifies. But the fact cannot be ignored that the Y-chromosome, so conspicuous in these insects, is absent in most forms, and we must therefore dismiss the possibility that the factors determining the testes of these insects are carried by this chromosome. The association therefore between the testes and the sex-chromosomes can be no closer than we have shown by experiment to be the case between the sex chromosomes and the other two exclusively male characters—the genital spot and the intromittent organ.

Realizing that the Y-chromosome cannot logically function as the carrier of the factors determining a male, Morgan '11 suggested that "the factors for producing the male must be in some other chromosome" (than the Y- or the X-chromosomes). We would consider this suggestion in relation to the factors determining the testes of these insects, ignoring for the present the fact that in his diagram illustrating this suggestion, Morgan does not place these factors in *one* chromosome but in a pair of chromosomes. If we attempt to place the factors for the testes in one of the autosomes, we meet difficulties that are quite as obvious as the difficulties in attempting to place the factors in the sex-chromosomes.

The above diagram (text Fig. 1) shows that the spermatozoa can be classed not only into two types (the so-called male-produc-

ing and female-producing), but each of these groups can again be separated into two types, in relation to their autosome content—one type containing the autosomes A, C, E, and the other type the autosomes B, D, F. As we are discussing the transmission of the testes, the factors for which are presumably carried by the male-producing spermatozoa, we shall consider the two types of these spermatozoa only—those with A, C, E, Y, and those with B, D, F, Y.

Our problem, as stated above, is to determine whether it is possible to place the factors which determine the testes of these insects in one of the autosomes.

A glance at text Fig. 1 shows that each of the autosomes is in *only half* the male-producing spermatozoa, and is also in half the female-producing spermatozoa. If, for example, we assume that autosome A carries the factors for determining the testes, and the X-chromosome carries the factors for determining the ovaries, we shall have *all* the female-producing spermatozoa carrying the factors for determining the ovaries, and in addition to this, half of these spermatozoa will carry the factors for determining the testes, as half of them have the A autosome. The male-producing spermatozoa, on the contrary, will not only carry none of the factors for determining the ovaries, but only half of them can carry the factors for determining the testes, as only half of them have the A autosome.

These conclusions, forced by an analysis of the chromosomes, are by no means in harmony with the demands of the chromosome sex-determination theory—thus it is quite as impossible to confine the factors for the testes to a single autosome, as we have shown is the case with the other two exclusively male characters—the genital spot and the intromittent organ. We might avoid this difficulty by assuming that the maturation divisions of one pair of the autosomes is like that of the XY-chromosomes, and that the factors for the testes are carried by one member of this pair. This involves, however, the further assumption that this autosome must follow the lead of the Y-chromosome or it might arrive in the female-producing spermatozoon. Unless we are willing to make some such unwarranted assumptions, it does not seem possible to make the association between the testes and

the sex-chromosomes any closer than we have shown by experiment is the case between these chromosomes and the genital spot and intromittent organ. Those who would place these factors in the chromosomes must concede that they must be in *at least* a pair of autosomes; there seems indeed no reason for assuming a different mode of transmission for the testes than for the other exclusively male characters—the genital spot and the intromittent organ. We feel we are therefore justified in our claim that the mode of transmission of the genital spot and intromittent organ is an index of the mode of transmission of the reproductive glands themselves, and that our cross-breeding experiments offer direct evidence against the chromosome theory of sex-determination.

If we reconsider Morgan's suggestion that "the factors for producing a male must be located in some other chromosome" than the X-chromosome, and we interpret "some other chromosome" as a pair of autosomes (as Morgan does in his formula) this would locate the factors for the testes in this pair of autosomes and be quite in harmony with our conclusions, that factors for exclusively male organs, if carried by chromosomes, cannot be in less than a pair of chromosomes—and it supports our claim that the method of transmission of the genital spot and intromittent organ is an index of the method of transmission of the testes.

#### Morgan's formula

Gametes of female—X M—X M

Gametes of male—X M—M.

gives the female zygotes ( $X M + X M$ ) just as many factors for "producing a male" (M M) as it gives for producing a female (XX) but he does not tell us what determines that the X gametes shall predominate.

According to Morgan's formula the term "female-producing spermatozoon" (X M) would appear to be a misnomer, for it carries "the factors for producing a male" as well as the factors for producing a female. The male-producing spermatozoon, on the contrary, carries the factors for producing a male only (M). The female-producing spermatozoon therefore can transmit exclusively male characters, as we have shown is the case, but

the male-producing spermatozoa cannot transmit exclusively female characters. That exclusively female characters and exclusively male characters should have such a different mode of transmission does not appear to us to be a logical conclusion, but it is a question that it is possible to put to the test of experiment.

The point of view of the investigator as to the chromosome theory of sex-determination seems to be entirely dependent upon the extent of his belief in the individuality of the chromosomes. In these insects, for example, the so-called male-producing spermatozoa have the Y-chromosome and not the X-chromosome, and those who believe in such a degree of individuality of the chromosomes as is demanded by the chromosome hypothesis of sex-determination, must hold that a so-called male-producing spermatozoon *must* develop into a pronucleus with a Y-chromosome and never an X-chromosome. They must hold that the Y- and X-chromosomes are as individual as the king and queen of chess for example.

On the other hand, the cytologist who believes that the chromosomes, like other organs in the cell, are the expression rather than the cause of cell activities, can also believe that there are forces outside the chromosomes that determine whether an egg shall develop into a male or female and can further believe that these forces, acting on the developing pronucleus can cause its chromatin content to develop into the chromosome configuration which is demanded by the sex. As it is impossible to follow the metamorphosis of a spermatozoon into a pronucleus, the cytological proof can probably never be achieved; but there is definite evidence that cells which normally produce certain organs, can be forced by experimental manipulation to produce other organs which have quite different functions, and such a change of function must create a corresponding change of structure, not only in the visible final result, but in the initial changes of the cell itself. Thus we believe that the structure of the cell, or any part of the cell is not the determining factor, but is merely an expression of other forces.

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## DESCRIPTION OF PLATE I.

The length of the intromittent organs was measured by a small pair of architect's dividers fitted with No. 9 needle points, and the dividers were frequently tested by measuring a 100 mm. line. Each intromittent organ was photographed at a magnification of 20 diameters, and the measuring was simplified by numbering each division of 20 mm. by a pencil mark. The measurements were taken from the distal end of the intromittent organ at the point where the coil enters the gland, the coil being easily dissected off at this point (photos 3, 4, etc.).

In photos 1, 2, 7, 9, a small part of the gland itself is retained. When part of the intromittent organ that is within the gland is preserved, the point from which the measurement was taken is easily determined, for the part within the gland is transparent and tapers at this point to a much smaller canal, *e. g.*, photos 15 and 19.

PHOTOS 1 to 4. Typical specimens of the intromittent organ of *Euschistus variolarius*. Length of the organ of photo 1, 98·5 mm. Photo 2, length 97·5 mm. Photo 3, length 95 mm. Photo 4, length 94 mm.

PHOTOS 5 to 8. Typical specimens of the intromittent organ of *E. servus*. Length of the organ of photo 5, 182 mm. Photo 6, length 158 mm. Photo 7, length 170 mm. Photo 8, length 162 mm.

PHOTOS 9 to 12. The intromittent organs from four of the F<sub>1</sub> hybrids. Length of the organ of photo 9, 124 mm. Photo 10, length 132 mm. Photo 11, length 122 mm. Photo 12, length 126 mm.

PHOTOS 13 to 20. The intromittent organs from eight of the F<sub>2</sub> generation. Length of the organ of photo 13, 85·5 mm. Photo 14, length 97 mm. Photo 15, length 140 mm. Photo 16, length 128 mm. Photo 17, length 147 mm. Photo 18, length 100 mm. Photo 19, length 124 mm. Photo 20, length 124 mm.

